



Separating effects of changes in atmospheric composition, climate and land-use on carbon sequestration of U.S. Mid-Atlantic temperate forests

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ABSTRACT

Terrestrial carbon dynamics have been vastly modified because of changes in atmospheric composition, climate, and land-use. However, few studies provide a complete analysis of the factors and interactions that affect carbon dynamics over a large landscape. This study examines how changes in atmospheric composition (CO₂, O₃ and N deposition), climate and land-use affected carbon dynamics and sequestration in Mid-Atlantic temperate forests during the 20th century. We modified and applied the PnET-CN model, a well established process-based ecosystem model with a strong foundation of ecosystem knowledge from experimental studies. We validated the model results using the U.S. Forest Inventory and Analysis (FIA) data. Our results suggest that chronic changes in atmospheric chemistry over the past century markedly affected carbon dynamics and sequestration in Mid-Atlantic temperate forests, while climate change only had a minor impact although inter-annual climatic variability had a far more substantial effect. The NPP response to a century of chronic change in atmospheric composition at the regional scale was an increase of 29%, of which, 14% was from elevated CO₂, 17% from N deposition, 6% from the interaction between CO₂ and N deposition, and minus 8% from tropospheric ozone. Climate change increased NPP by only 4%. Disturbed forests had 6% lower NPP than undisturbed forests after seven decades. Regrowing forests after harvesting and natural disturbances had much greater capacity for sequestering carbon than undisturbed old-growth forests even though the newer forests had slightly lower net primary production (NPP). The modeling results indicated that N deposition was a stronger force than elevated CO₂ for increasing NPP and fast turnover tissues, while elevated CO₂ favored more sustainable carbon storage and sequestration. The model results are consistent with various experiments and observations and demonstrate a powerful approach to integrate and expand our knowledge of complex interactive effects of multiple environmental changes on forest carbon dynamics.

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1. Introduction

Human activities have fundamentally changed the earth's surface and the chemical and physical climate (IPCC, 2008). These changes may interact in a complicated manner to affect productivity and carbon storage in forest ecosystems. The carbon dynamics of forests respond to climate, N deposition, elevated CO₂, tropospheric ozone, and land-use change (Aber et al., 2001; Ollinger et al., 2002a); however, there is uncertainty about the magnitude of responses to these factors, singly or in combination (Schimel, 1995; Vetter et al., 2005). The direct and secondary physiological effects of single-factor changes on plants and soils are known for many temperate forest species (Aber et al., 2001),

but knowledge of the effects of multiple interacting stresses across temporal and spatial scales remains elusive. In the last few decades, many bio-physiological experiments have been conducted at multiple scales that span tissue, plant, community and ecosystem levels of biological organization. These studies have generated abundant knowledge about the key mechanisms that explain how changing environmental factors interact to affect net photosynthesis and plant processes (McGuire et al., 1995). The knowledge and data gained from single-factor experiments at fine scales are considered sufficiently general to synthesize and extrapolate across broader scales, and to provide the foundation for quantitative models (Aber et al., 2001; Field et al., 1992).

Experimental studies have clearly shown that higher atmospheric CO₂ increases photosynthesis in plants, but at the ecosystem scale, it is uncertain whether this effect results in a lasting increase in sequestered carbon or causes a more rapid cycling of carbon between the ecosystem and the atmosphere (Körner et al., 2005; Lichter et al., 2005). Experiments have also shown that the effects of rising CO₂ are significantly moderated by

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increasing tropospheric ozone (Karnosky et al., 2003; Loya et al., 2003). When nitrogen is also considered, reduced soil fertility limits the response to rising CO₂ (Finzi et al., 2006; Luo et al., 2004), but N deposition can increase soil fertility to counteract this effect (Johnson et al., 1998; Magnani et al., 2007; Oren et al., 2001). All of these factors interact with climate. Of the many possible climatic variables, soil moisture availability has emerged as one of the key parameters regulating plant responses to elevated CO₂ and interacting with other factors (Karnosky et al., 2001; Oren et al., 2001).

The largest ecosystem-scale experiments generally manipulate only one or a few factors that can be easily controlled (DeLucia et al., 1999; Karnosky et al., 2003; Norby et al., 2005). Although we have learned a great deal from experiments, there are practical limits to understanding ecosystem responses to multiple factors from an experimental approach, and only for selected target ecosystems (Körner et al., 2005). Approaches based on observations of landscape-scale responses, such as regional forest inventories, likewise fail to provide much information to explain observed trends although the magnitude of all factors combined can be well defined and some of the obvious causes identified. For example, the effects of age-class and harvesting can be identified from inventories, but even these estimates include the effects of other factors that cannot be separated using just the inventory data (Birdsey and Heath, 2001; Pan et al., 2004a). Because of the complexity of interactions among multiple stresses, and the limitations of the experimental and observational approaches, models are often used to estimate or predict the specific causes of ecosystem-level responses. The most promising models are those built upon key physical and biological processes in ecosystems. Such “mechanistic” models can be used in a diagnostic sense to interpret temporal and spatial patterns of forest C dynamics, and for separating the effects of various climatic drivers and different environmental variables including CO₂ fertilization, N deposition and tropospheric ozone (Felzer et al., 2004; Nowak et al., 2004; Ollinger et al., 2002a; Pan et al., 1998, 2004b; Samuelson and Kelly, 2001). When multiple factors are considered, modeling studies generally show that the predictions of the effects are less than indicated by experiments involving one or a few factors (Schimel, 1995). Previous modeling studies have suggested that compared with human activities, the combined effects of climate and atmospheric chemistry changes on carbon sequestration of temperate forests are likely to be significantly less than the effects of land-use (Caspersen et al., 2000; Schimel et al., 2000). Several modeling studies in Europe suggest that the main driver of increased forest growth in the 20th century was increased nitrogen deposition, rather than the elevated CO₂ concentrations or climate change (Kahle et al., 2008; Magnani et al., 2007; Milne and van Oijen, 2005). However, it remains uncertain to what extent changing climate and atmospheric components have changed terrestrial carbon budgets (Schimel, 2007; Canadell et al., 2007a).

Few modeling studies have provided a complete analysis that attributes observed effects to multiple causes, partly because most ecosystem models do not have the “built-in” process-based functions for all the important environmental factors. In this study, we added new features to a well-known forest ecosystem model, PnET-CN, which has a unique capacity to explicitly analyze most changing environmental factors and to assess the interactive effects of elevated CO₂, atmospheric N deposition, tropospheric ozone, and historical climatic variability and land-disturbances on the carbon cycle. We used the modified model to explore the geographic complexity and variability of forest carbon dynamics under multiple stressors over the last century in temperate forests of the Mid-Atlantic region of the U.S. We designed factorial modeling experiments to examine single factors and combinations

of factors. Because we made multiple simulations leading to a complicated array of results, we chose to focus on analyzing responses of annual net primary productivity (NPP) and net ecosystem productivity (NEP) to climate variability and atmospheric components (CO₂, N deposition and ozone), and the interactions among these variables. NPP and NEP are two key variables revealing ecosystem functioning and carbon dynamics.

In this paper we attempt to answer several specific questions about the biological responses of forest ecosystems to multiple environmental changes and management history. What is the magnitude of enhancement by elevated CO₂ and N deposition, singly and interactively, on forest productivity and carbon sequestration in forest ecosystems? How much does tropospheric ozone act as a negative factor offsetting CO₂ enhancement at the ecosystem level? What are the impacts of climate and land-use change on forest carbon sequestration? What is the relative importance of each agent of change and their interactions on forest carbon dynamics in Mid-Atlantic temperate forests? The information from our integrated modeling approach is expected to increase understanding of these issues that are central to quantifying and predicting the response of terrestrial ecosystems to global change (Canadell et al., 2007a), and to present a methodology that may be useful in future reporting of the direct effects of human activity on the carbon cycle (IPCC, 2006).

2. Methods and data

2.1. Model description

The PnET-CN model (Aber et al., 1997; Ollinger et al., 2002a) is a process-based forest ecosystem model that simulates biogeochemical cycles (carbon, nitrogen, and water) in forest ecosystems at a monthly time-step. PnET-CN simulates the key physical and biological processes of northern temperate forest ecosystems, with parameters derived from a large amount of research results including long-term experiments at ecosystem scales (Aber and Melillo, 2001; Likens and Bormann, 1995). The model parameters are derived directly from field studies rather than calibrated; therefore, validation of the modeling results against empirical data is an important step to examine reliability and weakness in predictions.

The original version of PnET-CN was developed to provide understanding of the impacts of nitrogen deposition, tropospheric ozone, elevated CO₂ and land-use history on the carbon dynamics of northern hardwood forests in New England States (Ollinger et al., 2002a). We enhanced the model as a GIS modeling application in the Mid-Atlantic region at 1 km spatial resolution (approximately 284,000 pixels), and developed computer codes and parameters for simulating mixed forest types, particularly oak-pine forests in the region (Pan et al., 2004b). Detailed descriptions of the model are available elsewhere (Aber et al., 1997; Ollinger et al., 2002a; Pan et al., 2004b,c). Here we describe only a few of the key processes that are simulated.

In PnET-CN, atmospheric N deposition enters the forest ecosystems and accumulates in the available soil N pool. The nitrogen used for tissue construction is determined by rates of N uptake by plants and the ratios of carbon to nitrogen in different plant tissues (foliage, wood and roots). Elevated ambient CO₂ concentration has two impacts on carbon assimilation. It enhances C uptake by increasing the potential photosynthesis rate through a hyperbolic function (Ollinger et al., 2002a), and it reduces water conductance by the canopy. Trees exposed to high levels of ozone were reported to reduce photosynthesis because of direct cellular damage within leaves that inhibits stomatal conductance (Chappelka and Samuelson, 1998; Karnosky et al., 2003; Felzer et al., 2004). However, lower leaf conductance that is

caused by higher ambient CO₂ can down-regulate the O₃ damage (Samuelson and Kelly, 2001; Kolb and Matyssek, 2001; Ollinger et al., 2002a).

2.2. Data layers and scenarios

2.2.1. Vegetation, climate and soil data layers

The Mid-Atlantic region (Fig. 1, 35°00' to 47°30' N latitude, and 71°00' to 85°30' W longitude), covers 7 States in the Eastern U.S. and 460,000 km² of land, of which 64% is forest, 25% agricultural, 5% urban, 3% wetland, 2% inland water body, and 1% wasteland. Explicit geographically referenced data include forest types, monthly minimum and maximum temperature, monthly precipitation, monthly solar radiation, and soil water holding capacity (Fig. 1). In this study, U.S. Forest Service forest cover types (Zhu and Evans, 1994) were reclassified to the northern hardwood, spruce-fir, oak-hickory, pine, and oak-pine forest type groups (Table 1, Pan et al., 2004b, 2006). Oak-hickory is a dominant forest type in the Mid-Atlantic region, representing approximately 53% of the total forest area. The northern hardwood forest type covers about 29% of the forest area, with coniferous forest and mixed forest types each representing about 9% of total forest area. The data about soils and land-use history is documented elsewhere (Pan et al., 2004b,c). In brief, based on a general land-use history, we assumed that forests in the Mid-Atlantic region were established primarily from abandoned farmlands in the 18th century, and that the current forests are recovering from massive harvests that occurred in the

early 1930s. Forests also experienced a vast storm disturbance in 1950s in the region which affected about 5% of forests in terms of biomass removal. The climatic data used in this study include 30-year averages (1961–1990) and historical data (1895–2000). The spatial historical climate data were a combination of VEMAP data (1895–1980) (Kittel et al., 2001) and Daymet data (1980–2000) (Thornton et al., 1997). Although the VEMAP climate data covers 100 years from 1894 to 1993, they are at a coarse resolution (0.5°). Daymet data are at 1 km resolution that matches the resolution of our modeling needs and other data sets although limited to the period 1980–2000. Both datasets provide climatic anomalies of different variables (residuals) and we used them to overlay the regional average climate variables at 1 km resolution (Pan et al., 2004b) to obtain the transient climate data over the century. Climate variables shift seamlessly from VEMAP to Daymet data, indicating consistency of both climate datasets (Fig. 2a). Using these basic driving data sets, we ran the model for 200 years to initiate the simulation process (we used the regional mean climate data of 1961–1990 to spin-up the model run before 1895) and to fully incorporate the impacts of land-use over the past two centuries on biogeochemical cycles in forest ecosystems including agricultural practices and forest recovery from abandoned farm lands (Pan et al., 2004b).

2.2.2. Ozone data

We developed a high resolution (1 km) ozone data layer for the continental U.S. based on the raw data from the EPA ozone network

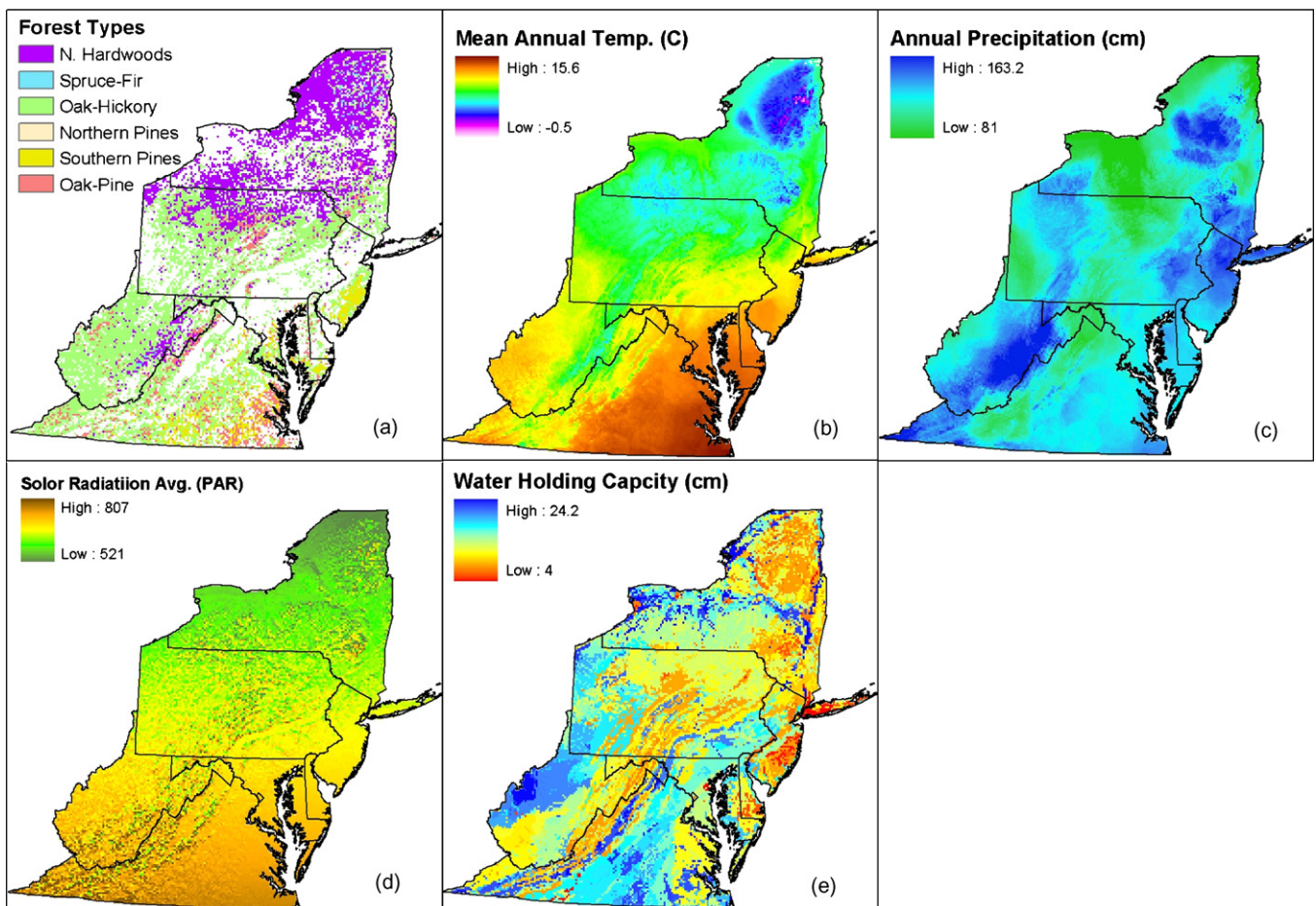


Fig. 1. The input data for the PnET-CN model. (a) Forest types; (b) mean annual temperature (the model used monthly minimum and maximum temperature data); (c) annual precipitation (the model used monthly precipitation); (d) mean annual photosynthetic active radiation (PAR) (the model used the monthly PAR); (e) soil water holding capacity. Note: The figure (b), (c) and (d) are only used for showing climate conditions in the region based on the annual means. The model uses the transient climate data at monthly step from 1895 to 2000 (see the data description).

Table 1

U.S. Forest Service forest cover types and the forest types used in PnET-CN.

Forest cover types	Percent of forest area	Forest types in the model	Percent of forest area
Maple-beech-birch	29	N. Hardwoods	29
Elm-Ash-cottonwood	<1		
Oak-hickory	53	Oak-hickory	53
Spruce-fir	1	Spruce-fir	1
White-red-jack pine	3	Pine Forests	8
Loblolly-shortleaf pine	5		
Long-leaf-slash pine	<1		
Oak-pine	8	Oak-Pine	9
Oak-gum-cypress	1		

collection stations (Fig. 2b, Prichard, 2003). Ozone effects on plant photosynthesis are based on cumulative ozone exposure during the day. PnET-CN uses the data known as D40 ppb, the sum of all hourly anomalies greater than the threshold of 40 ppb in the growing season. Because our data are SUM60 ppb, i.e. the sum of hourly values greater than 60 ppb, a non-linear regression between SUM60 and D40 was developed to convert the data of SUM60 to the model variable D40. We assumed that the tropospheric ozone was 10% of current concentration before 1931 and increased linearly to the present at a rate of approximately one percent per year

(Thompson, 1992). In the Mid-Atlantic region, ozone exposure is higher in the southern and coastal regions (Fig. 2b). The average level of ozone (SUM60) is about 31.3 ppb.

2.2.3. N deposition scenarios

Current patterns of wet nitrate (NO_3) and ammonium (NH_4) deposition were estimated from the average of 10 years (from 1990 to 1999) in order to dampen the order-of-magnitude variation recorded in wet and dry years. The 1-km resolution estimates were derived by interpolating the concentration data collected at National Atmospheric Deposition Project/National Trends Network monitoring sites, and the precipitation data from a denser network of National Atmospheric and Oceanic Administration Cooperative climatic sampling sites (Grimm and Lynch, 2004; Sheeder et al., 2002). Because there is no available regional data for dry N deposition, we calculated dry deposition for $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ using wet/dry ratios reported for the region's watersheds (Holland et al., 2005; Valigura et al., 2000). The regional average of total N deposition ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) from 1990 to 1999, including the dry and wet deposition, was approximately $10.3 \text{ kg N ha}^{-1}$. The N deposition varied across the region because of complex landscapes, rainfall patterns, and emission sources. Higher N deposition occurred in the higher elevations, areas with lake-effect precipitation, and western highlands, especially in

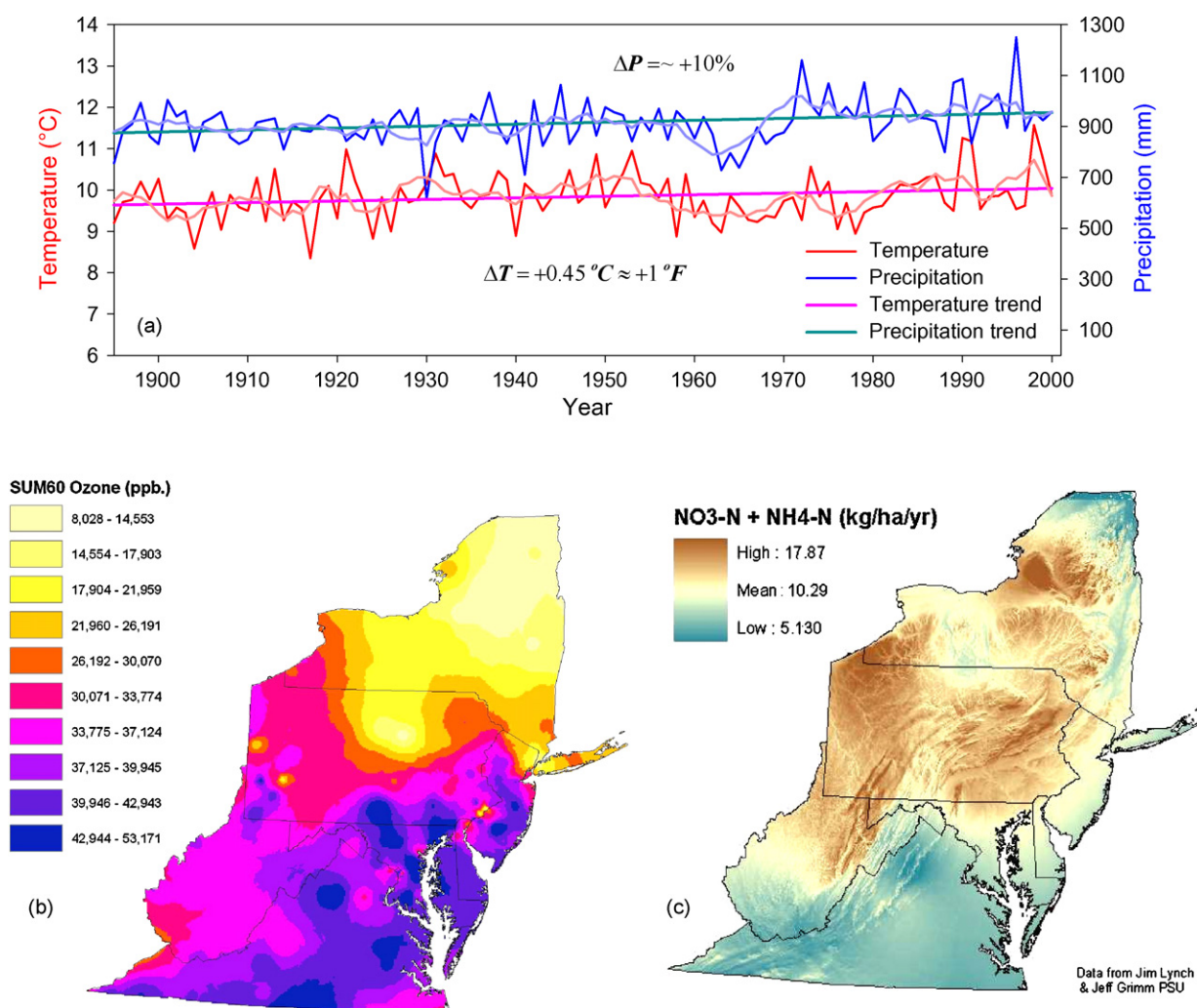


Fig. 2. Change in climate and atmospheric composition. (a) Climate variability and trends over 20th century (temperature and 5-year running mean, and trend; precipitation and 5-year running mean, and trend); (b) tropospheric ozone exposures SUM60 (May–September); (c) mean total annual wet and dry N deposition including NO_3 and NH_4 (1990–1999).

Pennsylvania (Fig. 2c). We assumed that N deposition before 1931 was approximately 20% of the average deposition from 1990 to 1999, which is roughly consistent with the rate of anthropogenic fixation of N in terrestrial ecosystems from pre-industrial time (Galloway et al., 1995). We also assumed that the deposition rate increased linearly from 1931 to 1990. This linear relationship was interpolated for the simulation years based on the specific value at each pixel. Although N deposition varies yearly, we used this simple approach because spatial N deposition data are lacking before 1990.

2.2.4. CO₂ scenarios

The scenario for atmospheric CO₂ concentration is based on the Mauna Loa record and not spatially differentiated. The elevated CO₂ increased linearly from 280 ppm of the pre-industrial level to 369 ppm in 2000 (<http://cdiac.ornl.gov/ftp/trends/co2/mauna-loa.co2>) and is considered as being well mixed.

2.3. Factorial modeling experiments and the variables used in analyses

The modeling factorial experiments were designed to examine individual and combined effects of alternative atmospheric chemistry scenarios on Mid-Atlantic temperate forests. The model was run for the scenarios of control (pre-industrial condition), increased N deposition only, elevated CO₂ concentration only, elevated ozone concentration only, elevated CO₂ concentration plus N deposition, elevated CO₂ concentration plus ozone, and a full scenario of increased N deposition, CO₂ and ozone. The whole set of factorial modeling experiments for atmospheric composition was also run under average climate and historical climate (to include inter-annual variability), and with and without land disturbances. Therefore, a total of 28 modeling runs were performed. The various modeling experiments tested the model's sensitivity to different control factors, and provided modeling results to investigate possible effects of environmental changes on temperate forest carbon dynamics in the Mid-Atlantic region.

Although the model can simulate many important variables of ecosystem carbon fluxes and pools, we focused our analyses mostly on annual net primary productivity (NPP) and annual net ecosystem productivity (NEP) because NPP is the most direct indicator of plant carbon assimilation, and NEP indicates the net carbon gains in the ecosystem. In the model, monthly net carbon balance is calculated as the difference between monthly net photosynthesis and plant respirations (for growth and maintenance) plus soil respiration (Aber et al., 1997). Growth and maintenance respirations are estimated respectively as the fractions of photosynthetic variables or biomass production, varying with different plant tissues (foliage, fine roots, and wood); and soil respiration is defined as a function of soil temperature. Annual NEP is the sum of the monthly net carbon balance. For comparing the values at a regional scale, we used the averaged NPP and NEP of the last 10 years of the model simulations (1991–2000) for evaluating the effects of changing atmospheric components because otherwise annual climate variability may confound such a comparison. To help understand the pattern of how forest ecosystems sequestered carbon over several decades, we used the cumulative NEP (CNEP) to show the effects from changes in climate, atmospheric composition and land-use. We also detailed the effect on CNEP attributed to N deposition, elevated CO₂, and increased tropospheric O₃. We only investigated the carbon sequestration dynamics over 70 years in order to compare regrowth forests and old-growth forests that did not experience harvests in 1930s and storm disturbances in 1950s.

2.4. Model validation and comparison

Validation gives us a measure of how robust the model performs and the degree of uncertainty in predictions (VEMAP, 1995). If our model predictions match the data well, we have confidence in the results and a strong basis for gaining insights about effects of multiple interacting stresses on forests, in the absence of empirical studies. We compared the modeling results with two data sources: the annual NPP estimates based on forest inventory and field data for forest types in the Mid-Atlantic region (Jenkins et al., 2001; Pan et al., 2006; White et al., 2000), and the biomass data from Forest Inventory Analysis data (FIA) (Bechtold and Patterson, 2005). The details describing how to develop NPP validation data are documented in previous work (Pan et al., 2006). The FIA biomass data were based on inventories around 2000 (Bechtold and Patterson, 2005). Biomass is more directly estimated from the FIA data than NPP, which requires estimates of change in biomass as well as litter production and fine root turnover. However, since the FIA biomass is essentially an estimate of stem biomass, we calculated branch, foliage and stump/root biomass using the method and indices provided by Wharton et al. (1997) to get total forest biomass. We summarized the FIA total forest biomass and the modeled total forest biomass at a state level based on forest types for comparison.

2.5. Analysis of variance for the process-based model results

We conducted additional statistical analysis using the procedure of mixed ANOVA to examine how the multiple driving factors affect the modeled NPP and NEP results from the factorial modeling experiments. For consistency and simplifying statistical data, we only used the simulation results of 10 years (1991–2000) to formulate ANOVA. The mixed ANOVA provides information about relative statistical importance of each driving factor and their interactions based on the amount of variation contributed and reflected in the dependent variable NPP and NEP.

3. Results

3.1. Validation of the modeled results using forest inventory data

The measurement-based NPP and biomass data were used as the benchmark for comparison with the modeling results. The comparison indicated that the NPP estimates from the PnET-CN model generally agree very well with the inventory based estimates, with slightly overestimated NPP for deciduous forests, and narrower standard deviations for coniferous/mixed forests. The small variation in the modeled NPP, especially for coniferous/mixed forests, reflects the impacts of the model parameters which are based on averages for the region, and the use of spatially smoothed climatic and soil data (Pan et al., 2006) (Fig. 3a). The validation of biomass at a state level based on forest types indicates that the model can predict forest biomass with acceptable accuracy (Fig. 3b). The model again overestimated biomass of deciduous forests, and predicted a smaller standard deviation for coniferous forests, similar to the conclusion from the validation of NPP (Pan et al., 2006). However, we suspect that significant subregional uncertainty exists that is masked by validation at the large scale represented by the FIA data.

3.2. Temporal and spatial response of NPP to multiple environmental changes

Under pre-industrial conditions in the absence of disturbance, the mean regional NPP is 765 g m⁻² (Table 2). With chronic

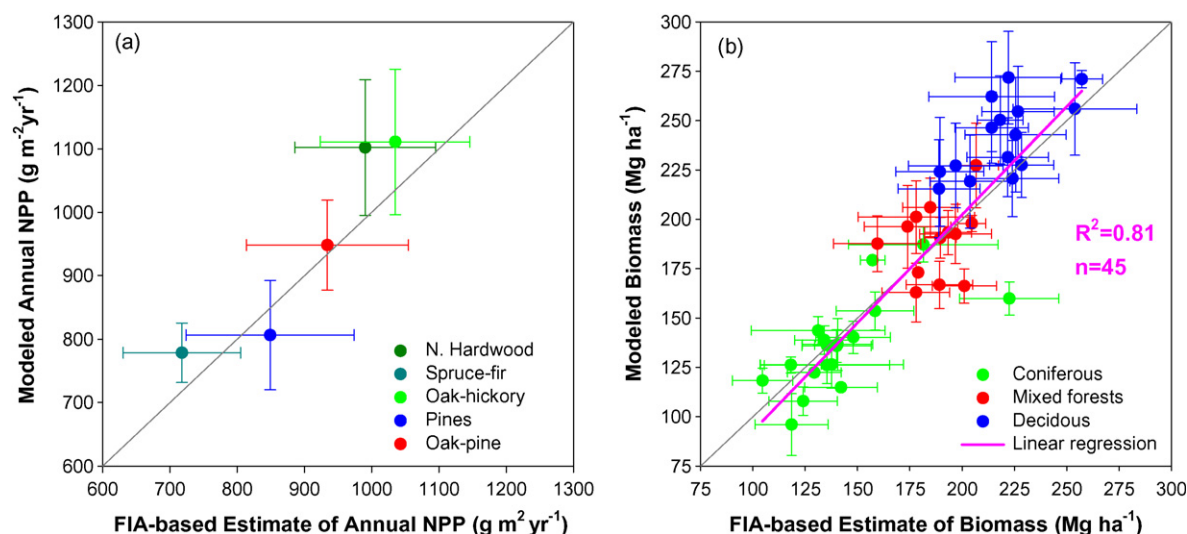


Fig. 3. Validation of the model results using Forest Inventory and Analysis (FIA) data: (a) annual NPP estimates of forest types in the Mid-Atlantic region; (b) Biomass estimates of forest types based on averaged values from seven states in the Mid-Atlantic region (the details were described in the text).

changes of atmospheric components in the past decades, NPP increased by 14% under elevated CO_2 , 17% under increased N deposition, and 37% under elevated CO_2 plus N deposition. Both CO_2 and N are considered as limiting elements for plant growth, and the interactive effect between elevated CO_2 and N deposition increased NPP by an extra 6%, possibly from a better balance of C and N in plants. Tropospheric ozone only reduced NPP by 7%, but offset more than half of the CO_2 enhancement of NPP when combined with elevated CO_2 . The overall impact from a full scenario of changing atmospheric composition resulted in 29% increase in NPP of Mid-Atlantic temperate forests. With disturbances, effects of change in atmospheric composition are slightly different, because young forests may react differently than old-growth forests to biochemical requirements for tissue construction. The impact of N deposition on younger forests is slightly higher (20% vs. 17%). While the effect of elevated CO_2 and higher tropospheric ozone remain almost the same individually, the combination of the two factors reduces ozone damage. As a result, the total effect from changing atmospheric composition was to increase NPP by 32%, slightly higher than the effect for undisturbed forests. When only considering the effect of disturbances (comparing two control scenarios), i.e. the events of harvesting and storm damage in the 1920s and 1950s (Pan et al., 2004b), NPP was only reduced by about 6% at the end of the century (Table 2). Over the century, forest NPP increased significantly with changes in atmospheric composition (Fig. 4a) and seemed to reverse a natural trend of decline with forest aging.

To identify the effect of climate variability and long-term change, we compared simulations using historic transient climate and average climate data. The NPP residuals from the model simulations between historical climate and average climate were

mostly negative values, particularly for deciduous forest types. However, we are mainly interested in the changing trend of NPP, which reflects the net effect of climate change on NPP. The results show a slight increase in regional NPP, about 4% over the century, possibly the outcome of a rising temperature (0.45°C or $\sim 1^\circ\text{F}$) and precipitation (10%) (Figs. 2a and 5a). The 10-year running means of NPP residuals reveal a 25-year cycle of weather with a slightly increased trend and amplitude (Fig. 5b).

Decadal snapshots of NPP spatial distributions show that regional patterns of NPP in different years have high variability (Fig. 6). Generally, NPP is affected by combined conditions of temperature and moisture, e.g. higher in northern areas near the Great Lakes and lower along the Appalachian ridges and in the southeastern sandy coastal plain. However, NPP distribution patterns were greatly affected by inter-annual variability of climate across geographic terrains, as shown by generally lower NPP in 1990, and relatively higher NPP in 1980 and 2000.

3.3. Net ecosystem productivity (NEP)

Net ecosystem productivity (NEP) increased under changes in atmospheric composition. NEP increased by 138–208% depending on disturbance scenarios (Table 2) and ended up higher in the regrowth than undisturbed forests ($162\text{ g m}^{-2}\text{ yr}^{-1}$ vs. $123\text{ g m}^{-2}\text{ yr}^{-1}$). NEP appears to have larger inter-annual fluctuations and is also smaller in magnitude than NPP since it is largely controlled by ecosystem respiration which is more sensitive to climate variability (Fig. 4b). NEP declined over the century as forests aged. With disturbances, NEP increased immediately, then reduced and bounced back in following years (Fig. 4b) for increased woody debris and soil respiration; and recovered young forests

Table 2

Regional summary of responses of NPP and NEP to altered atmospheric composition (means of 1991–2000).

Scenarios	NPP-ND ($\text{g m}^{-2}\text{ yr}^{-1}$)			NPP-DS ($\text{g m}^{-2}\text{ yr}^{-1}$)			NEP-ND ($\text{g m}^{-2}\text{ yr}^{-1}$)			NEP-DS ($\text{g m}^{-2}\text{ yr}^{-1}$)		
Control	765			723			40			68		
N_{DEP}	891	+17%		865	+20%		47	+18%		90	+32%	
CO_2	874	+14%		818	+13%		112	+180%		129	+90%	
O_3	709	–7%		672	–7%		10	–75%		41	–40%	
$\text{CO}_2 + \text{O}_3$	801	+5%		776	+7%		71	+78%		109	+60%	
$\text{CO}_2 + \text{N}_{\text{DEP}}$	1051	+37%		1012	+40%		156	+290%		193	+184%	
$\text{CO}_2 + \text{N}_{\text{DEP}} + \text{O}_3$	990	+29%		955	+32%		123	+208%		162	+138%	

ND means forests were undisturbed during the simulations and DS means forests were harvested and regrowing during the simulations.

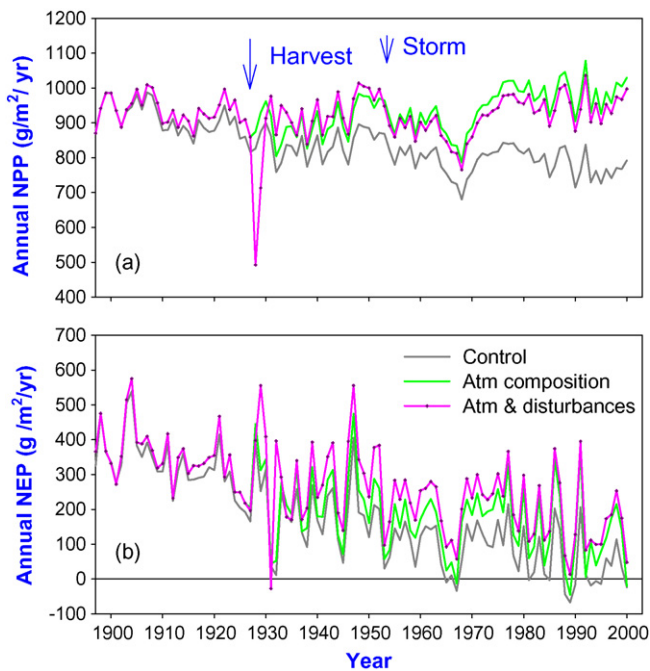


Fig. 4. Carbon dynamics of Mid-Atlantic temperate forests over the 20th century: (a) modeled annual net primary production (NPP); (b) modeled annual net ecosystem production (NEP). Gray line, the control condition without change in atmospheric composition and disturbances; green line, with change in atmospheric composition; pink line, with change in atmospheric composition and disturbances (harvest and storm).

eventually achieved higher NEP for lower maintenance respiration and faster carbon assimilation. However, for the region, even though NPP was enhanced by changes in atmospheric composition and showed an increasing trend, NEP showed a long-term declining trend (Fig. 4). This suggested that NPP and NEP are not always concurrent because of influence by different control

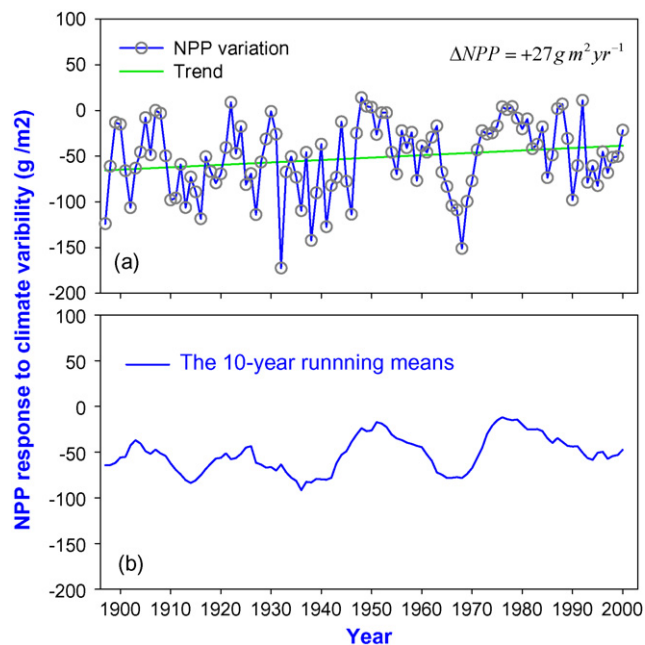


Fig. 5. NPP responses to inter-annual climate variability and change: (a) NPP residuals responding to climate variability and trend; (b) the 10-year running means of NPP residuals.

factors. This situation is very evident by comparing NPP and NEP maps for the year 2000 (Fig. 6).

3.4. Differences of NPP responses among forest types

Forest types responded differently to climate and altered atmospheric composition. Deciduous forests have higher NPP than coniferous forests (Table 3) and appear to be more sensitive to climate variability (Fig. 7a). Different forest types responded in various ways to the change in long-term climate trends. Oak-hickory had a positive response (+6%), pines had almost no response (−0.1%), and spruce-fir and northern hardwood forests had a slightly negative response (−4% and −2% respectively) to the climate changes over the century (Fig. 7a). The impacts of atmospheric composition (N deposition, CO₂ and ozone) on annual NPP are positive for all forest types (Fig. 7b) and increased by 24% for northern hardwood, 30% for spruce-fir, 30% for oak-hickory, 42% for pine, and 37% for oak-pine forests (Table 3). Among deciduous forests, the results revealed that NPP of northern hardwood forests (mainly maple-beech-birch forests) had a higher response to elevated CO₂ (17% vs. 10%) and a lower response to N deposition than the southern oak-hickory forests (13% vs. 18%) even though the northern hardwood forests likely received a higher amount of N deposition (11.1 kg N ha^{−1} vs. 10.3 kg N ha^{−1}, see Fig. 2). Among coniferous types, pines had much higher response to N deposition than to elevated CO₂ (28% vs. 16%), the highest response to N deposition among all forest types. The few spruce-fir forests found in northern mountainous region had more comparable responses to N deposition and elevated CO₂ (15% and 13% respectively). Oak-pine forest, a mixed forest type, appears to have as a high response as pine types to N deposition (25%), but low response as oak-hickory type to elevated CO₂ (12%). Ozone reduced about 7–8% of NPP for most forest types except Spruce-fir forests that seem more resistant to ozone damage (−1%).

3.5. Attribution of the regional NPP and carbon accumulation to various causes

Additional analysis of NPP responses (for all factors, some not shown in Table 2) and attribution to various causes (Fig. 8) are summarized here: change in climate increased NPP by 4%, disturbances decreased NPP by 6% (compared to non-disturbed old-growth forests), elevated CO₂ increased NPP by 14%, ozone decreased NPP by 7%, ozone and CO₂ had a slight negative interaction and reduced NPP about 2%, N deposition increased NPP by 17%, and a positive interaction of elevated CO₂ and N deposition increased NPP by 6%. All changes in atmospheric composition taken together resulted in a total NPP increase of 29%, and changes in climate and atmospheric composition together increased regional NPP by 34% over the century. The results mentioned here were based on the simulations using the undisturbed scenario except for the estimation of the disturbance effect (−6%).

The cumulative NEP (CNEP) results (Fig. 9) show that, in general, regrowth forests had sequestered more carbon than old-growth over decades. Carbon accumulated over 70 years in old-growth forest averaged about 3433 g C m^{−2}. Of this amount, regular growth accounted for 2171 g C m^{−2}, change in atmospheric composition contributed 1128 g C m^{−2}, and change in climate added 134 g C m^{−2}. The regrowth forest accumulated 4408 g C m^{−2} over the period. Of this total accumulation, regrowth accounted for 3072 g C m^{−2}, change in atmospheric composition contributed 1230 g C m^{−2}, and change in climate only added 106 g C m^{−2}. Overall, regrowth forests had a greater capacity for carbon accumulation, which was 28% higher than old-growth forests. Without considering the impacts from change in atmosphere composition and climate, regrowth could more effectively

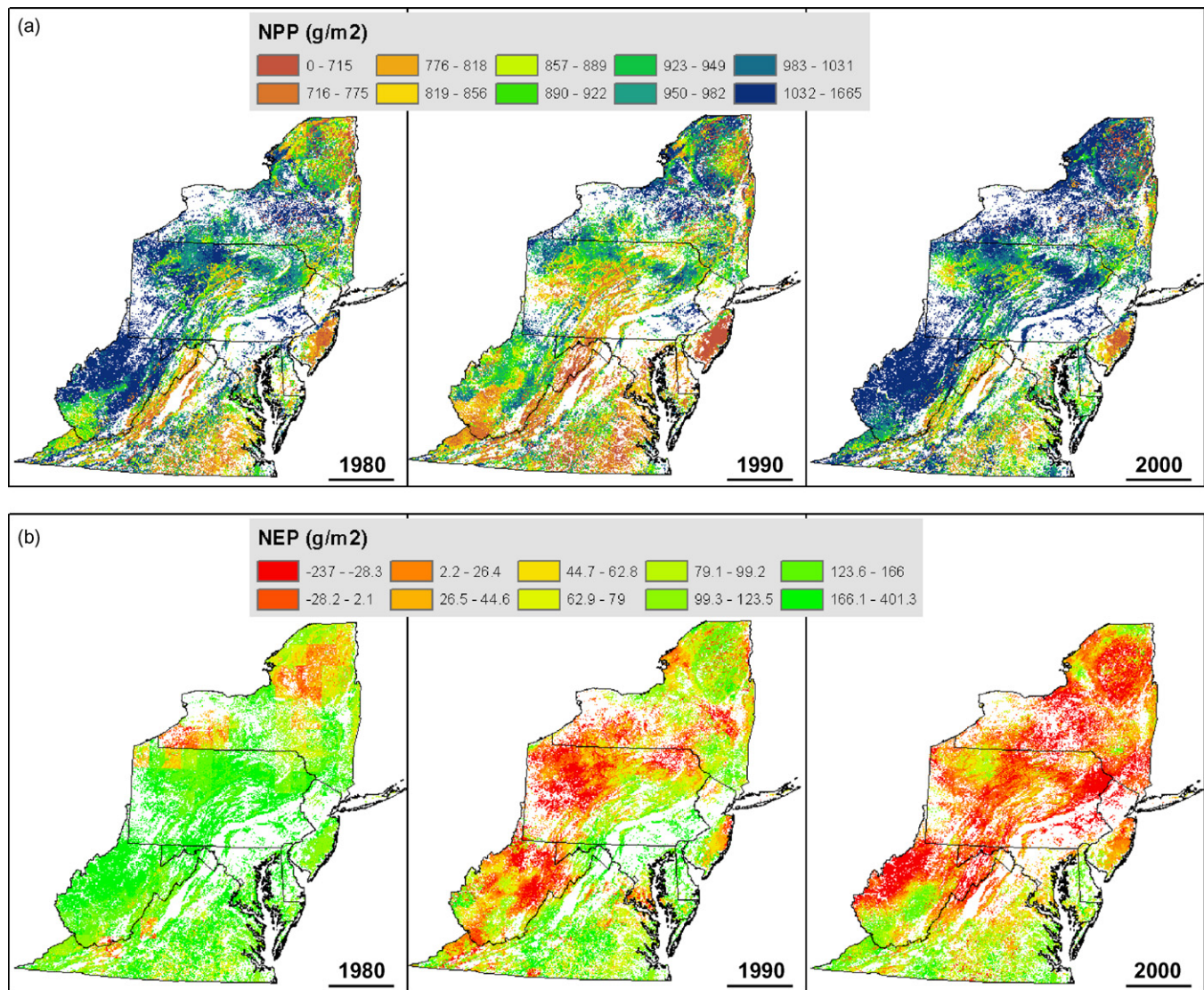


Fig. 6. Decadal snapshots of spatial patterns of forest NPP and NEP in the Mid-Atlantic region (a) NPP in 1980, 1990 and 2000; (b) NEP in 1980, 1990, and 2000.

sequester carbon, which was about 42% higher than the old-growth. Comparatively, changes in atmospheric composition and climate contributed a greater fraction to carbon accumulation in old-growth forests (37% vs. 30% in regrowth forests). However, the change in atmospheric composition was a strong factor. The effect can be further partitioned (Fig. 9c and d), suggesting that a major factor for increasing carbon sequestration in forest ecosystems was elevated CO₂; N deposition and the interaction between CO₂ and N could add a similar amount of carbon accumulation (~43% and 48% of total effects of elevated CO₂ and N deposition); but a negative effect from tropospheric ozone offset about a half of the CO₂ fertilization effect (Fig. 9c and d).

3.6. Statistical significance of the effects of environmental factors on NPP and NEP

The mixed ANOVA results (Table 4) quantify the statistical significance of the effects of multiple environmental factors and the interactions on NPP and NEP. For the dependent variable NPP, it shows that changes in atmospheric composition (CO₂, N and O₃) and transient climate (vs. mean climate to account the averaged effects of the climate trend and variability) all have significant effects. Among them, N deposition has the greatest impact, then

elevated CO₂, climate and ozone. The only significant interaction is between elevated CO₂ and N deposition, while the remaining interactions among different factors are statistically insignificant. The residual is the accumulated variation that cannot be interpreted by the factors and interactions, which should be mainly related to the inter-annual variations of all NPP variables over 10 years (the autocorrelation should be small because only 10 years' data were applied), and accounts for about 12% of the total variation.

NEP, the indicator of carbon sequestration, appears to be affected differently by the driving factors. Only elevated CO₂ and climate have significant impacts on NEP, whereas N deposition, ozone and the interaction between climate and N have minimally significant effects (Table 4). The interaction between climate and N deposition produces some effect on NEP likely because N deposition level is associated with precipitation and could dampen carbon storage in woody product when it is too high (Pan et al., 2004b). However, the residual takes a major portion of the total variation (74%), suggesting the inter-annual variation dominates NEP more than any other effects. Overall, the statistical ANOVA is consistent with our independent analysis by comparing the mean values (1991–2000) of the factorial modeling experiments (Table 2).

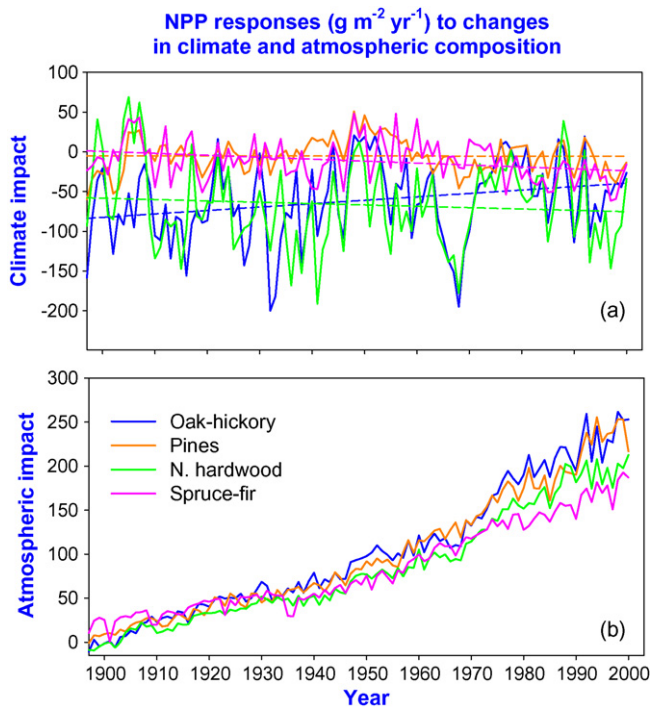


Fig. 7. NPP responses of different forest types to change in climate and atmospheric composition. (a) NPP residuals related to climate variability and change. The trends of change vary among the forest types. (b) NPP changes related to change in atmospheric composition.

4. Discussion

Well-built process-based ecosystem models should capture key ecosystem processes and interactions of terrestrial ecosystems with environmental forcing factors (Field et al., 1992), and predict quantitative consequences of any single factor or combination of factors. Ecosystem models should also reflect current rates of forest productivity following the accumulated long-term increase in stressors. A solid validation of the PnET-CN simulations with measured data from forest inventory and remote sensing for forest cover types (this study and Pan et al., 2006) shows that PnET-CN is a reliable forest ecosystem model for diagnosing and predicting large-scale impacts of environmental changes on forest carbon dynamics in the Mid-Atlantic region. Based on this evidence, we highlight a few essential issues that emerged from our comprehensive analyses of the model results.

4.1. Changes in atmospheric composition alter carbon allocation patterns

Different responses by carbon variables (NPP and NEP) may indicate altering biomass allocation in trees because of elevated CO₂ and N deposition. The results indicate that forests respond to increased N and CO₂ by increasing NPP; however, nitrogen

deposition has a stronger effect than elevated CO₂ on forest net primary productivity (NPP), but less effect on net ecosystem productivity (NEP) (Table 2) and therefore cumulative carbon in ecosystems (Fig. 9c and d). Such an inference is also suggested by statistical analysis (Table 4). This may imply that N deposition stimulated greater production of fast turnover tissues such as foliage and fine roots, while elevated CO₂ likely enhanced more sustainable products such as woody biomass. Because the C:N ratios vary in plant tissues (McGuire et al., 1997; Ollinger et al., 2002b), roots and foliage are resource-acquiring tissues, and have lower C:N ratios than woody biomass. Thus, these tissues have priority for utilizing acquired N (Grime et al., 1984; Chapin, 1980). With additional N input to forests, more carbon products are likely allocated to roots and foliage to balance higher N concentration in these tissues (Field et al., 1992; Chapin et al., 1990). Our modeling results are consistent with evidence from ¹⁵N-tracer experimental studies, which indicate that tree biomass is not a primary sink of atmospheric N deposition in northern temperate forests (Nadelhoffer et al., 1999). As our other study suggested, extra N deposition potentially has a negative impact on forest biomass, likely because it diverts carbohydrates allocated to wood production (Pan et al., 2004b). Most of the stimulated production of foliage and fine roots contributes to the forest soil C pool. Foliage and fine roots typically have faster turnover compared to wood, thus could be more susceptible to changing climate.

On the other hand, elevated CO₂ initially decreases N concentration in foliage (Yin, 2002) and increases foliage production (roots may also respond this way because foliage and roots may be closely linked). However, after the C:N ratios in foliage/roots reach their peaks, the extra carbon product is allocated to woody tissue that has lower priority for carbon allocation and has a large potential to accumulate carbon with a high C:N ratio. Because biomass pools of foliage and roots are small and relatively stable, the enhanced carbon product due to elevated CO₂ can be mostly transferred to woody tissue. The predicted ecosystem responses by the model reflect mechanisms at the plant level that regulate resource and control primary production through variation in biomass and nutrient allocation (Field et al., 1992; Dickson et al., 2000).

4.2. Interacting effects of changes in atmospheric composition

Factorial modeling experiments enable generation of sufficient information to examine single, combined and interacting mechanisms of changing environmental factors and provide insights for understanding the effects of complex multiple stresses on carbon dynamics in forest ecosystems (Mooney et al., 1991). Both elevated CO₂ and ozone act by directly affecting photosynthesis and stomatal conductance. Elevated CO₂ stimulates photosynthesis, suppresses stomatal conductance and causes higher water use efficiency in plants (Mooney et al., 1999; Pan et al., 1998). Ozone exposure at high levels generally reduces photosynthesis by direct damage to stomata (Reich, 1987; Felzer et al., 2004). Low stomatal conductance due to elevated CO₂ or drought can down-regulate the negative effect from ozone (Ollinger et al., 2002b; Reich, 1987;

Table 3
Response of NPP by forest types to changes in atmospheric composition.

Scenarios	Northern hardwood	Oak-hickory	Spruce-fir	Pines	Oak-pine
Control	811	792	580	558	674
N _{DEP}	+10%	+18%	+15%	+28%	+25%
CO ₂	+17%	+13%	+13%	+16%	+12%
O ₃	−8%	−8%	−1%	−7%	−7%
CO ₂ + O ₃	+8%	+3%	+12%	+9%	+4%
CO ₂ + N _{DEP}	+33%	+38%	+32%	+49%	+43%
CO ₂ + N _{DEP} + O ₃	+24%	+30%	+30%	+42%	+37%

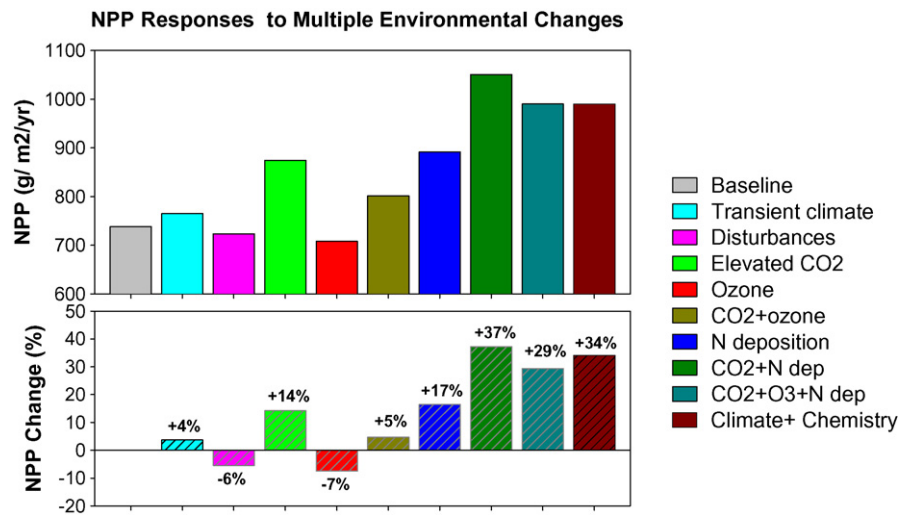


Fig. 8. Average forest NPP of the latest decade of 20th century under various scenarios and the NPP responses resulted from the modeling factorial experiments. These results enable factoring out the effect of changes in atmospheric composition, climate and land disturbances.

Reich and Amundson, 1985). However, a high water use efficiency associated with elevated CO₂ conserves water and alleviates water stress, and in turn may adjust conductance in an opposite way and increase the ozone impact. The paired impacts depend on interactions among direct and indirect effects of elevated CO₂ and ozone on photosynthesis, canopy conductance and water balance. However, the modeling results in this study indicate that ozone may reduce about 45% (in disturbed forests) to 65% (in old-growth forests) of the CO₂ enhancement benefit (Table 2). Ozone seems to consistently reduce NPP by 7–8% for all forest types except spruce-fir which appears to have little ozone response, possibly because spruce-fir forests are mostly located in the

northern high elevations and exposed to a low ozone level (Figs. 1a and 2b). The Aspen-FACE studies with 6 years' elevated CO₂ and tropospheric ozone treatments demonstrated more dramatic responses of NPP to elevated CO₂ and ozone than our modeling results. In the experiment, the average effect of elevated CO₂ increased NPP by 51%, elevated O₃ reduced NPP by 18%, while the concurrent exposure to elevated CO₂ and O₃ only increased NPP by 13%. (King et al., 2005). The NPP response to elevated CO₂ was reduced by about 20% by interacting with O₃, though the statistical ANOVA results indicate there is no significant interaction between the CO₂ and ozone treatments (King et al., 2005), a similar conclusion as our ANOVA of the modeling results. In total, about

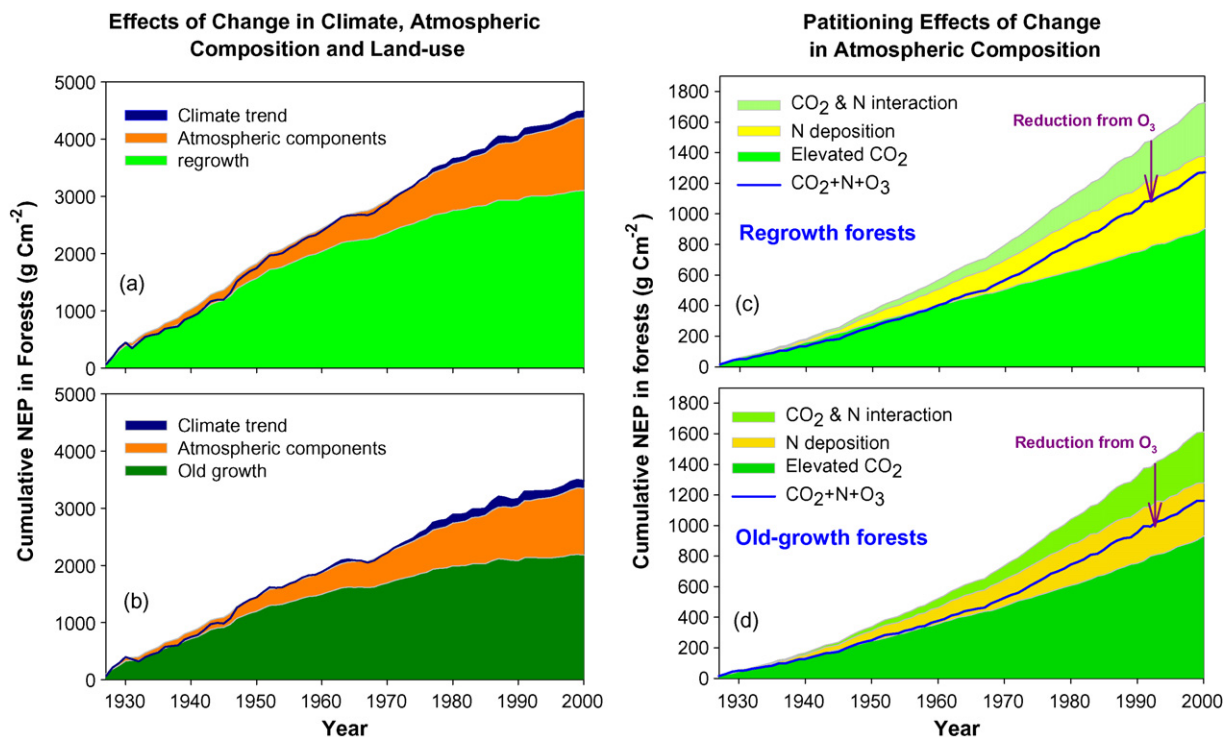


Fig. 9. Cumulative NEP (g C m^{-2}) in forests, which reflects carbon sequestration in forest ecosystems. (a) Effects of regrowth (disturbed forests), climate change and atmospheric composition change; (b) effects of old-growth (undisturbed forests), climate change and atmospheric composition change; (c) partitioning the effects of change in atmospheric composition in regrowth forests; (d) partitioning the effects of change in atmospheric composition in old-growth forests.

Table 4

The mixed analysis of variance (ANOVA) for the modeled NPP and NEP results, summarizing the effects of multiple environmental factors and their interactions.

Source of variation	DF	NPP			NEP		
		SS	Contribution of variation (%)	P	SS	Contribution of variation (%)	P
CO ₂	1	330,162	28.04	<0.001**	35,746	16.81	<0.001**
N deposition	1	482,136	40.95	<0.001**	4,549	2.14	0.153*
Ozone	1	74,245	6.31	<0.001**	4,621	2.17	0.150*
Climate	1	131,330	11.15	<0.001**	5,540	2.60	0.057**
CO ₂ × N interaction	1	15,012	1.27	0.003**	1,575	0.74	0.398
CO ₂ × O ₃ interaction	1	620	0.05	0.540	175	0.08	0.778
N × O ₃ interaction	1	306	0.03	0.667	114	0.05	0.820
CO ₂ × O ₃ × N interaction	1	82	~0.01	0.823	5	~0.00	0.962
Climate × CO ₂ interaction	1	44	~0.00	0.818	120	0.06	0.699
Climate × O ₃ interaction	1	704	0.06	0.358	175	0.08	0.712
Climate × N interaction	1	27	~0.00	0.866	2,925	1.38	0.120*
Climate × CO ₂ × O ₃ interaction	1	1,422	0.12	0.192*	112	0.05	0.768
Climate × CO ₂ × N interaction	1	311	0.03	0.524	110	0.05	0.761
Residual	126	141,016	11.98		156,904	73.78	
Total	139	1,177,107	100.00		212,670	100.00	

* Statistically not very significant but having some effects.

** Statistically significant.

75% of CO₂ fertilization benefit of NPP is diminished by ozone exposure in the Aspen-FACE experiment. The stronger responses of aspen forests (pure and mixed types) both to CO₂ and O₃ are simply due to the higher CO₂ and ozone treatment levels in Aspen-FACE, both about 50% higher than the ambient levels, while the model incorporates the chronic increases over a century from the pre-industrial levels to the ambient levels, with the annual increase rate of 0.4% and 1% respectively for CO₂ and O₃.

The interactive effect between elevated CO₂ and increased N deposition is more remarkable and statistically significant (Table 4). Under either an enriched CO₂ or N environment where these factors have the opposite effects on leaf nitrogen concentration (McGuire et al., 1995), the carbon and nitrogen tend to compensate for each other's imbalance through allocation regimes over a range of C:N ratios, eventually restricting biochemical capacity for photosynthesis when another resource reaches the point of limitation (Field et al., 1992; Chapin et al., 2002). When elevated CO₂ and N deposition occur simultaneously, better balanced supplies of CO₂ and N generally increase growth potential and sink strength through their interacting effects. Our results indicate that an interacting effect of elevated CO₂ and N deposition on NPP is an average increase of 6–7%, varying slightly among forest types (4–7%) (Table 3). A lower C:N interactive effect on coniferous forests may relate to wider ranges of C:N ratios in coniferous trees that have greater plasticity responding to the individual resource (C or N), often as a consequence of adapting to low resource environments (Grime, 1977; Chapin, 1980; Chapin et al., 1993; Tilman, 1990; Field et al., 1992; Reich et al., 1995).

4.3. Carbon dynamics and sequestration in Mid-Atlantic temperate forests

The chronic changes in atmospheric composition in the past decades markedly affected carbon dynamics and sequestration in Mid-Atlantic temperate forests. Increased N deposition and ambient CO₂ fertilized those forests, while tropospheric ozone exerted negative impacts through foliar damage. Under complete scenarios of changing atmospheric composition, NPP increased by 29% in old-growth forests and by 32% in regrowth forests at a regional scale (Table 2). Tropospheric ozone reduced 7% of NPP on average, which affected all other forest types except spruce-fir forests that may have less exposure to this pollutant. The change in climate (temperature and precipitation) over a century seems to only account for a small change in NPP, an increase of about 4%,

although inter-annual variability had much greater effect on NPP and particularly NEP on a yearly basis (Figs. 4 and 5).

Our modeled NPP under an average climate was generally higher than under a transient climate, which is unlike many other models that often produce intermediate values when using average climate date. We consider our result reasonable because an average climate may act as an optimal climate in a region. A process included in the PnET-CN model makes a “bad” weather year decrease NPP and also reduce labile carbon reserves in plant storage tissues that will be used for producing new leaves in the subsequent year, thus affecting next year's NPP. A “good” year may not totally reverse this lagging effect. Therefore, an average climate can cause higher NPP without the depreciative effects of an unfavorable growth year.

As to the regional response to the trend of climate, which is small (+4%), the responses of different forest types in the region are mostly diverse, from positive (oak-hickory), nil (pine) to negative response (Spruce-fir and northern hardwood) (Fig. 7a). Because oak-hickory forest distributions are in more southern areas (Fig. 1), the positive response to climate could be related to the precipitation increase that was high in that region. The negative NPP responses of northern hardwoods and spruce-fir forests to climate change could be more related to the change in temperature because forests adapted to colder environments may not always benefit from higher temperature, particularly with warmer nights and milder winters (Alexander et al., 2005). Pine forests are usually found in less fertile soils, such as sandy coastal regions. While increasing precipitation could benefit NPP of pines in general, increasing temperature at nights and in the winter may increase the maintenance respiration that could offset the improved precipitation condition. As the result, there is almost no effect of climate change on NPP trend of pines. However, even though oak-hickory forests responded most positively to changing climate (+6%), the effect is quite insignificant compared to the effects of inter-annual variability of climate and effects of the change in atmospheric composition (Fig. 7a and b).

From the perspective of increasing biochemical capacity for photosynthesis, the modeling results suggest that N deposition is a stronger force than elevated CO₂ for increasing primary production for most forest types. In our study, the only exception is the northern hardwood forest with greater NPP response to elevated CO₂, which we believe is partially related to its special phenology (Pan Y., unpublished data). This conclusion is consistent with the European studies that reported ca. 20% enhancement in observed

forest productivity from increased N deposition (Kahle et al., 2008; Rehfuss et al., 1999) and was considered the most important factor driving carbon sequestration in temperate and boreal forests (Magnani et al., 2007).

But, our results reveal that the “fertilization” effect of N deposition mainly stimulates C allocation to short-lived tissues such as foliage and fine roots. These tissues eventually contribute to soil organic matter, but likely have fast turnover rates (Nadelhoffer et al., 1999). In contrast, the “fertilization” effect by elevated CO₂ likely enhances more sustainable C storage such as woody biomass (including coarse roots). FACE studies (mostly using much higher CO₂ concentration for experiments than ambient level) reported a 23% increase in NPP under high experimental CO₂ concentration and suggest that elevated CO₂ significantly enhanced cumulative woody tissues and had relatively low carbon allocation to fine roots (Oren et al., 2001; Norby et al., 2005). However, the evidence indicated that CO₂ enhancement of photosynthesis could decline over time as other resources become less available, especially in N-limited ecosystems (Luo et al., 2004; Finzi et al., 2006; Norby et al., 2008). When elevated CO₂ interacts with increased N supply by N deposition, saturation thresholds for either CO₂ or N are released, producing substantial increases in C sequestration. In spite of that, ozone pollution offsets about 21% of enhanced biochemical capacity for photosynthesis due to elevated CO₂ and N deposition (Table 2).

We also found that regrowth forests had stronger capacity for accumulating carbon over decades than old-growth forests although the old-growth seems to continue being a carbon sink (Luyssaert et al., 2008). The forest regrowth scenario (without considering impacts from changes in atmospheric composition and climate) showed a near doubling of the capacity of the old-growth (42%) to sequester carbon. However, the old-growth forest was likely approaching an equilibrium status for storing more carbon, while the regrowth forest had higher capacity to store more carbon during the simulation period but was approaching its maximum storage level at the end of the 20th century (Fig. 9a and b). Change in atmospheric composition (from elevated CO₂ and N deposition) stimulated a much greater carbon sequestration in forest ecosystems, which was 40% of total carbon sequestration in the regrowth forest and 52% in the old-growth forest. Also, elevated CO₂ played a stronger role than N deposition for carbon sequestration in forests (Fig. 9c and d). In addition to forest regrowth that played a dominating role for the forest carbon sink of the continental U.S. in the last century (Pacala et al., 2001; Birdsey et al., 2006), our results indicate that the change in atmospheric composition, particularly elevated CO₂, will gradually account for more of the carbon sink of temperate forests in the Mid-Atlantic region in the future. Such a significant “fertilization effect” on the forest carbon sequestration could eventually result in a “greener world” after a long period of chronic change in atmospheric composition and cumulative impact. Although change in climate in the region had only a minor effect on increasing forest carbon sink over the century, it could become more significant in the future as the change in climate becomes more dramatic, even though it is uncertain whether the effect would be a positive or negative on terrestrial carbon budget.

Our results have important implications for development of new reporting protocols for greenhouse gas inventories and registries. Attributing the effects to different causes allows assessing the magnitude of impact of each factor. One of the more difficult challenges in reporting schemes has been to separate out the effects of natural causes (e.g., climate variability) and indirect human causes (e.g., increasing CO₂) from the direct impacts of land management decisions such as converting non-forest land to forest (Canadell et al., 2007b,c). Most of the current greenhouse gas registries and reporting systems are based on an

inventory approach that accounts for all causal factors combined. The “Good Practice Guidance” for greenhouse gas inventories developed by the Intergovernmental Panel on Climate Change approximates the direct human effects by separating land into “managed” and “unmanaged” categories (IPCC, 2006), but in reality there are multiple factors affecting changes in carbon stocks on all lands. A credible modeling approach is likely to be the only way to separate out factors in such a way that reported changes could be focused on the direct human impacts. The results of this study indicate that, for the Mid-Atlantic Region of the U.S., the direct effect of land management (regrowing forests) is about 70% of the total effect of all factors combined (Fig. 9). A similar logic may be applied to different combinations of factors depending upon how the reporting rules are written.

Our study demonstrated the quantitative changes in the carbon cycle of Mid-Atlantic temperate forests in response to multiple stresses caused by changing atmospheric chemistry and climate. The model results show the reasonable strength of the mechanistic approach using process-based models to study complex interactive effects of multiple environmental factors on forest carbon dynamics (Rastetter et al., 2003) and the capacity for separating the effects of different causes. The strength of modeling research provides a unique opportunity to expand our knowledge on analyzing complex relationships among interacting factors. The insights we gained from the analysis cannot be derived from manipulative experiments because their complexity would be impractical and too costly to implement (Aber et al., 2001). The flexibility in modeling research can partially supplement weakness in experimental studies, but can never substitute for field experiments. After all, the best mechanisms built into ecosystem process models are based on results of experimental studies, and should be continuously validated by real data under more complicated design and experimental manipulations.

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